

Effects of Weather on Breeding Ducks in North Dakota

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By Merrill C. Hammond
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by

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Abstract

The present report quantifies relations between weather and several aspects of the breeding biology of four duck species: mallard (*Anas platyrhynchos*), gadwall (*A. strepera*), blue-winged teal (*A. discors*), and redhead (*Aythya americana*). Data were obtained from two locations in North Dakota,—the J. Clark Salyer National Wildlife Refuge, intermittently during 1936-68, and the Northern Prairie Wildlife Research Center's Woodworth Station during 1965-77. Arrival dates varied with mean temperature before and during the usual arrival period; early-arriving species were affected by early-season temperatures, and later-arriving species by temperatures later in spring. After temperature effects were accounted for, first arrivals were seen at the more southern Woodworth Station a few days earlier than at Salyer.

High spring temperatures also seemed to induce early nesting. The mallard, which nested earliest, was most affected by temperatures during April, whereas the other species were most affected by temperatures during late April and May. Peak hatching dates were also earlier in years with higher temperatures in May. Earlier peaks were associated with early first nests, so it was difficult to separate the effects of weather and date of initial nesting. Peaks at Woodworth occurred earlier than at Salyer, after temperature differences were taken into account. The period of most active nesting was longest for the early-nesting mallard, shortest for the late-nesting gadwall, and intermediate for the blue-winged teal and redhead. For two species, precipitation during the breeding season may have prolonged nesting activities. We also found that late nesting seasons tend to be compressed.

Productivity at Salyer, measured by the brood to pair ratio, was generally greater in years with higher temperatures during 23 April-3 June. Effects were more pronounced among early-nesting species. Average brood size for Classes I and II tended to decline during the 1947-62 period at Salyer; pair populations generally increased. Consequently, it was nearly impossible to distinguish the effects of pair density on brood size from those of yearly trend. In addition, Class II broods were smaller in years when temperatures were higher during late May and June.

The dependence of waterfowl on aspects of spring weather for the timing of arrival and the onset of breeding activities has long been part of biological folklore. Despite an awareness of these associations, relations between weather and waterfowl biology have rarely been quantified, partly because studies were too short to elucidate clear dependencies. We examined the effects of temperature and precipitation on waterfowl arrival, nesting, and production on two breeding areas

in North Dakota. Dates of arrival, initiation of first nests, and peak hatching, as well as length of period of most active nesting, productivity, and brood size, were studied in the mallard (*Anas platyrhynchos*), gadwall (*A. strepera*), blue-winged teal (*A. discors*), and redhead (*Aythya americana*).

Study Areas

The areas we studied were on the J. Clark Salyer National Wildlife Refuge (Salyer) in Bottineau and

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McHenry counties, and at the Woodworth Station, a field station of the Northern Prairie Wildlife Research Center in Stutsman County, about 200 km southeast of Salyer. Basic climatological information is provided in Table 1; further details were presented by Jensen (1972).

Wetlands at Salyer are mainly impounded marshes managed with water control structures on the Souris River. At Woodworth, however, the wetlands are natural and include most of the classes described by Stewart and Kantrud (1971), although only a few are semipermanent or permanent.

Methods

Weather Data

We obtained weather data from the monthly and annual publications of the National Oceanic and Atmospheric Administration, National Climatic Center, Asheville, North Carolina. Weather information pertinent to Salyer was recorded at Upham; that for Woodworth was recorded at the station or at nearby towns.

Weather data were tabulated as weekly averages of daily maximum, minimum, and mean temperatures, and of total precipitation during the week. We discovered during preliminary analyses that the average daily mean temperature adequately represented that aspect of weather, so minimum and maximum temperatures were not considered further.

Duck Arrival Dates

The first ducks of each species to arrive in spring were recorded at both study areas. Although a more representative measure of arrival might have been the

Table 1. *Climatological information for the Salyer and Woodworth study areas.*

Climatological information	Study area	
	Salyer ^a	Woodworth ^b
Mean temperature (°C)		
March	-7.6	-5.7
April	3.7	4.6
May	11.0	11.4
June	17.0	17.3
Mean precipitation ^c (cm)		
March	5.1	5.1
April	6.4	8.4
May	13.0	14.2
June	23.9	21.8

^aSalyer elevation = 434 m.

^bWoodworth elevation = 582 m.

^cInterpolated from graphs in Jensen (1972).

date on which the first major influx appeared, this measure is more subjective and, in most years, the first ducks seen and the first waves to arrive were separated by only a few days.

Breeding Pair Populations

During 1949-54, pair counts were made at Salyer on a sample of wetland areas and were nonstatistically projected to the entire refuge. During 1955-63, ducks were censused on virtually the entire refuge; methods used were similar to those described by Hammond (1969).

Pair counts were systematically made at Woodworth during May 1965-77. All wetland basins containing water were surveyed.

Nesting Studies and Brood Counts

Nesting studies were performed at Salyer and Woodworth to obtain information on dates of first nest initiation and peak hatching, and span of nesting.

Brood surveys were the most important source of data for brood size analysis, nesting chronology and, in conjunction with estimates of the breeding population, productivity rate. Guides by Gollop and Marshall (1954) and Hammond (1970) were used for conducting brood surveys.

Broods at Salyer were censused from a boat or canoe powered by an outboard motor through open water channels of the marshes. Time of day, date, weather requirements, and scanning points were standardized. During the 14-year span of taking brood counts at Salyer, marsh vegetation gradually encroached on some of the better brood areas, making observation difficult. We suspect that estimates of productivity during 1958-62 were low compared with those made during 1949-57.

Brood counts were made at Woodworth each July by performing a "beat-out," in which many people simultaneously plodded through each wet pond or walked shorelines to record all broods or hens exhibiting broody behavior.

Broods of different species vary in time spent on the water and in their preference for emergent vegetation. For these reasons, greater proportions of broods were observed for some species (e.g., gadwalls and redheads) than for others (e.g., mallards and blue-winged teal).

We constructed nesting chronology curves by back-dating broods observed. These curves contain data representing only successful nests. Any cause of nest loss, such as predation, that was both appreciable and variable among years would modify the curve and possibly mask effects of weather. The long span of the study made such variability likely.

We used nesting chronology curves to estimate date of first nest initiation, date of peak hatching, and span of the nesting period, but recognized that an observed curve of nesting chronology might not reflect the actual curve because of losses that occur. We were unable to determine the date of first nest initiation at Woodworth because of limited samples.

Ducks at Salyer were subjected to two influences, botulism and flooding, that did not markedly affect those at Woodworth; predator reduction occurred in both areas. Botulism outbreaks occurred in one or two marsh units in 1949, 1959, and 1960. Productivity data were gathered from other areas whenever possible. Flooding on the Souris River and its tributaries occasionally inundated low-lying nesting habitat and depressed nesting success and productivity. Predation was fairly intense at Salyer and probably was more so at Woodworth. It was countered by various predator control methods; in some years, strychnine-treated eggs were used at Salyer, and shooting and trapping occurred on both areas.

Data Analysis

We employed the simplest methods of analysis adequate for the task. For example, we treated each species individually—although a multivariate approach might yield more powerful hypothesis tests, we chose the single-species approach to highlight important distinctions among the species.

Results and Discussion

Duck Arrival Dates

The arrival date—the day on which an individual of a species was first observed on the study area—was subject to some variability. An aberrant value could be recorded if an unusually early migrant was seen a week or more before others of that species. Such observations were uncommon among our data; in most years the arrival of the first single bird was followed by a wave of birds within a few days.

Mallard

Mallards arrived on the median date of 30 March at Salyer and 20 March at Woodworth (Table 2). Annual variation in arrival dates was considerable, however, ranging from 7 March to 10 April at Salyer and from 15 March to 6 April at Woodworth.

The arrival of mallards in spring was strongly influenced by temperatures during the usual arrival period. Arrival tended to be later when temperatures were low during 12 March–8 April (Fig. 1a). Arrival dates were delayed an average of 1.8 days ($P < 0.0001$) for each Celsius degree difference in the mean temperature. A more detailed examination showed that mean temperatures during 12–25 March accounted for most of the variation in arrival dates.

Table 2. Summary statistics of breeding activities of four duck species at the Salyer (S) and Woodworth (W) study areas. Dates are Julian.

Activity	Species and study area							
	Mallard		Gadwall		Blue-winged teal		Redhead	
	S	W	S	W	S	W	S	W
Arrival (n ^a)	28	13	29	13	28	12	29	10
Median	89	79	102.5	97	105.5	101.5	98	94.5
Mean	86.7	83.6	102.2	94.8	105.4	102.5	98.3	94.3
SD ^b	7.7	8.8	7.9	9.9	5.8	4.9	7.6	8.5
Initiation (n)	25	—	25	—	26	—	11	—
Median	109	—	137	—	130	—	123	—
Mean	108.4	—	132.4	—	128.9	—	126.8	—
SD	7.8	—	7.9	—	7.1	—	13.8	—
Peak hatching (n)	18	—	19	10	19	12	18	—
Median	176	—	190	180.5	185.5	180	193	—
Mean	176.5	—	189.8	183.6	186.3	178.3	191.1	—
SD	10.6	—	6.3	9.6	6.9	5.6	10.1	—
Span (n)	18	—	19	10	19	12	10	—
Mean	46.6	—	32.9	30.6	34.7	38.1	37.7	—
SD	5.9	—	4.8	6.2	4.2	7.3	7.9	—

^an = number of years.

^bSD = standard deviation.

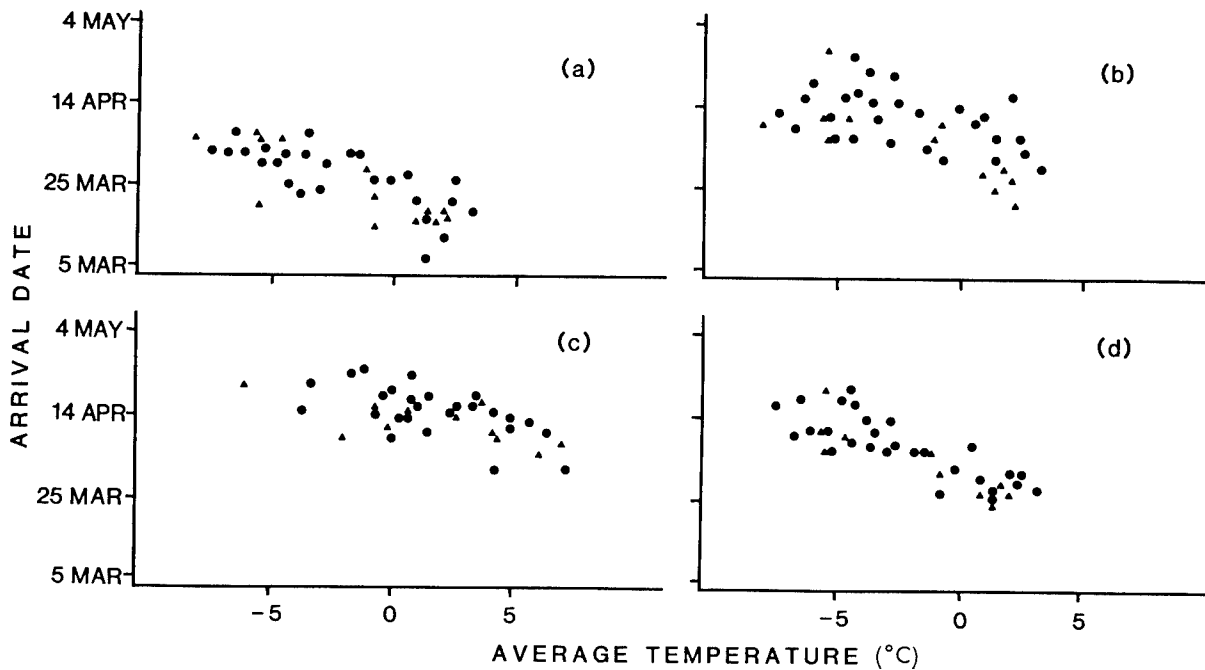


Fig. 1. Arrival date in relation to average temperature ($^{\circ}\text{C}$) during 12 March–8 April for mallard (a), gadwall (b), and redhead (d); and during 26 March–15 April for blue-winged teal (c); dots denote Salyer, triangles denote Woodworth.

Arrival dates at Salyer and at Woodworth tended to be similar when mean temperatures were similar (Fig. 1a). The difference adjusted for mean temperatures was 1.8 days earlier at Woodworth, which was not significant ($P = 0.30$). Thus the 10-day difference in median arrival dates between the two areas was largely due to the earlier warming at Woodworth than at Salyer.

Gadwall

The median dates of gadwall arrival were 12–13 April (range, 30 March–2 May) at Salyer and 7 April (range, 20 March–28 April) at Woodworth (Table 2). The arrival of gadwalls was also influenced by low temperatures during the usual arrival period (Fig. 1b). Gadwalls arrived an average of 1.46 days later for each Celsius degree change in mean temperature during 12 March–8 April ($P < 0.0001$). Temperatures during the latter part of that period were particularly influential.

Unlike the mallard, the gadwall seemed to arrive significantly ($P < 0.01$) earlier at Woodworth than at Salyer under similar temperature regimes (Fig. 1b). The estimated difference in arrival dates between the two areas, adjusted for mean temperature, was 6.0 days.

Blue-winged Teal

The median arrival date of blue-winged teal (Table 2) was 15–16 April at Salyer (range, 1–25 April) and 11–12 April at Woodworth (range, 5–22 April). Blue-winged teal were influenced in their arrival by low temperatures (Fig. 1c), particularly during 26 March–15 April. Arrival dates were delayed 1.07 days for each Celsius degree difference in mean temperature during the period ($P < 0.0001$). Under similar temperatures, blue-winged teal seemed to arrive somewhat earlier at Woodworth than at Salyer; the adjusted difference was 2.5 days earlier at Woodworth ($P = 0.12$).

Redhead

Median arrival dates of redheads (Table 2) were 8 April at Salyer (range, 26 March–21 April), and 4–5 April at Woodworth (range, 25 March–21 April). Redheads tended to be delayed by low temperatures (Fig. 1d), particularly during 12 March–8 April. They were delayed 2.0 days for each Celsius degree difference in mean temperature ($P < 0.0001$). Under similar temperature conditions, redheads arrived at Woodworth somewhat earlier (2.4 days; $P = 0.14$) than at Salyer.

General

Below-normal temperatures during or just before the typical arrival period tended to delay arrivals for each of the four species. The earliest arriving species, the mallard, was particularly influenced by temperatures during 12–25 March. The next earliest, the redhead, was apparently affected by temperatures during 12 March–8 April. The third species to arrive, the gadwall, had arrival dates most strongly related to mean temperatures during 26 March–8 April. The latest of the four species, the blue-winged teal, had arrival dates correlated with temperatures during 26 March–15 April.

In addition to effects of mean temperatures, differences in arrival date were observed between Salyer and Woodworth. Under similar weather regimes, birds of each species could be expected earlier at Woodworth. The difference was 1.8 days for mallards, 2.4 days for redheads, 2.5 days for blue-winged teal, and 6.0 days for gadwalls, only the last being clearly different from zero.

These findings corroborate the common notion that late, cold springs result in delayed arrivals of migrating ducks. Sowls (1955) suggested that later-arriving species were less affected by temperatures than the early-arriving mallard and pintail, but this contention was not supported by our data. Arrival date is determined by weather patterns throughout the migrational corridor during the entire period of migration; temperature at the terminus can only account for a portion of the variation.

Breeding Pair Populations

Counts of breeding pairs are available for Salyer during 1949–63 and for Woodworth during 1965–77 (Table 3). All species varied in number from year to year. Coefficients of variation for the four species averaged 36% at Salyer and 41% at Woodworth; numbers of redheads were particularly variable at Woodworth.

The four species tended to vary together from year to year. Numbers of mallards, gadwalls, and blue-winged teal at Salyer averaged higher in 1956–63 than in 1949–55; redheads did not exhibit this trend. All species at Woodworth were more abundant during years of good wetland conditions and less abundant when many ponds were dry.

Species Composition (%) of these four species was different at the two study areas:

	Blue-winged			
	Mallard	Gadwall	teal	Redhead
Salyer	19.0	23.5	47.1	10.4
Woodworth	14.7	19.0	62.4	4.0

Woodworth had proportionately more blue-winged teal and fewer redheads than Salyer.

Nest Initiation Dates

The week in which the first egg was laid by a species was estimated from backdating either broods observed

Table 3. Summary statistics of abundance of four duck species at the Salyer (S) and Woodworth (W) study areas. Brood to pair ratios are $\times 1,000$ for Salyer and $\times 100$ for Woodworth.

Abundance	Species and study area							
	Mallard		Gadwall		Blue-winged teal		Redhead	
	S	W	S	W	S	W	S	W
Breeding population (n ^a)	15	13	15	13	15	13	15	13
Mean	1,022	54	1,263	70	2,533	229	559	14
SD ^b	329	13	534	17	745	86	218	11
CV ^c (%)	32	24	42	24	29	38	39	79
Broods (n)	14	13	14	13	14	13	14	13
Mean	9.9	12.8	66.9	22.9	72.9	84.7	19.9	3.4
SD	8.0	8.0	51.3	10.5	85.6	48.0	17.2	2.6
Ratio (n)	14	13	14	13	14	13	14	-
Mean	10.3	27.1	65.3	36.0	31.9	39.4	38.5	-
SD	7.4	19.4	72.0	21.3	43.2	21.0	35.8	-

^an = number of years.

^bSD = standard deviation.

^cCV = coefficient of variation.

or nests found. Nests or broods could be lost before they were observed, therefore the initiation dates of nesting were estimated in the field only to within a week, and subtle differences among years may have been obscured. For analysis, these dates were converted back to the Julian date of the middle day of the week.

We sought to determine if any relation existed between date of nest initiation and weather variables, as summarized by the mean temperature during the weeks when first nests are initiated. We also explored effects of arrival date on first nest initiation: If birds arrive late do they also begin to nest late? Data were available only from Salyer.

Mallard

The median week that mallards initiated nests was estimated at 16–22 April (Table 2), but ranged from 2–8 April to 30 April–6 May. The difference between median arrival date and date of nest initiation was 20 days. The initiation date was compared with mean temperatures during 2 April–6 May, the period in which mallards began to nest (Fig. 2a). The regression coefficient, -0.77 , was not significant ($P = 0.28$).

Gadwall

Gadwalls initiated first nests primarily during the weeks of 7–13 May and 14–20 May, but in some years

they began about 2 weeks earlier to 1 week later. Nest initiations were significantly ($r = -0.488$; $P < 0.02$) delayed by low temperatures during 16 April–27 May (Fig. 2b), the period in which initial gadwall nests were detected. We attributed no additional effects to arrival date which preceded first nests by an average of 34.5 days. The regression coefficient of -2.15 suggested that the first nest was delayed by slightly more than 2 days for each Celsius degree change in average temperature during the period of initial nesting.

Blue-winged Teal

Blue-winged teal began their first nest during the week of 7–13 May in most years, but variations of about a week were not uncommon. Nesting began about 24.5 days after arrival. The date of nest initiation among blue-winged teal was related ($r = -0.563$; $P < 0.01$) to average temperatures during 16 April–27 May, the period of initial nesting (Fig. 2c). Again, no additional effects were attributed to arrival date. The regression coefficient of -1.97 suggested a change of nearly 2 days in nest initiation for each Celsius degree change in average temperatures.

Redhead

First nests of redheads were started from the week of 16–22 April to the week of 28 May–3 June; little clumping about the mean was evident. On the basis of

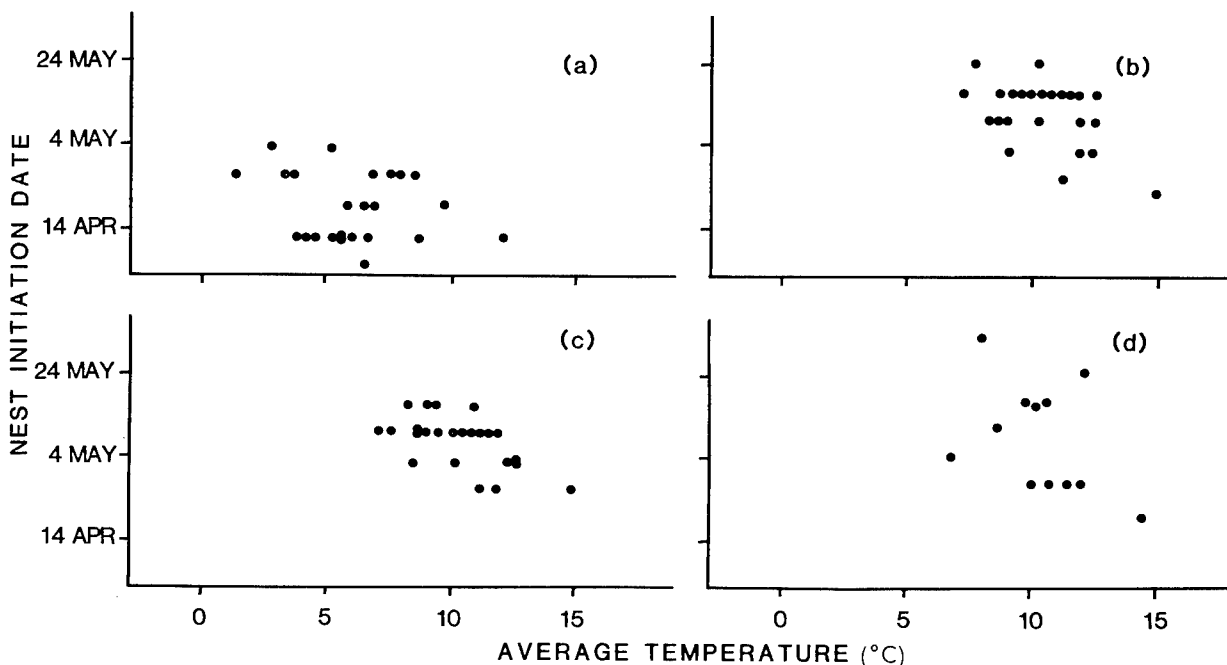


Fig. 2. Nest initiation date in relation to average temperature ($^{\circ}\text{C}$) during 2 April–6 May for mallard (a) and 16 April–27 May for gadwall (b), blue-winged teal (c), and redhead (d).

11 years of data, the difference between median arrival date and first nest initiation was 25 days. First nests were recorded later when temperatures were lower during 16 April–27 May (Fig. 2d), but not significantly so ($r = -0.439$; $P = 0.18$). The regression coefficient was -2.84 days per Celsius degree.

General

All species seemed to delay nest initiation under low temperature conditions, but the effect was significant only among gadwalls and blue-winged teal. For mallards the delay was 0.77 day per Celsius degree difference in mean temperatures during 2 April–6 May. Temperatures during 16 April–27 May were influential for the other species, and delays (in days per Celsius degree difference) were 2.15 for gadwalls, 1.97 for blue-winged teal, and 2.84 for redheads.

Much has been written about possible influences of weather on nest initiation. Delays associated with cool springs and late ice melt have been reported for mallards (Ogilvie 1964; Nilsson 1974; Milne 1976) as well as for geese (MacInnes et al. 1974; Raveling 1978) and other waterfowl. Specific instances were described by Dane (1966), who suggested that blue-winged teal delayed nesting in 1963 because of a period of cold weather in late April and early May, and by Harris (1954), who observed that several species nested late in 1950, a year with a cold and dry spring. Coulter and Miller (1968) indicated that more American black ducks (*Anas rubripes*) nested early when March temperatures were above normal than when they were below normal, but the difference was only marginally significant ($P = 0.12$).

Several investigators performed analyses comparable to ours, or provided data in sufficient detail that we could analyze them. Data from Newton and Campbell (1975) yielded a correlation between the date of first clutch and mean February temperature of $r = -0.850$ ($P < 0.05$) for a population of mallards that initiated nesting in March. For later-nesting species, the onset of nesting seemed independent of weather.

Keith (1961) noticed no consistent relation between nesting phenology and the temperature and precipitation variables he considered. A reexamination of his data showed, however, that mallards, gadwalls, blue-winged teal, northern pintails (*Anas acuta*), and redheads all nested later in 1953–54 than in 1955–57. Temperatures during April and May averaged higher during 1955–57 than during the previous 2 years; this relation is consistent with our conclusions.

A reanalysis of Yocom's (1950) data on mallards, gadwalls, teal (blue-winged and cinnamon [*Anas cyanoptera*]), and redheads showed that the date of initiation of each species during the 3 years of study was negatively correlated with mean temperatures during April and May. The eight correlation coefficients aver-

aged -0.76 . We also reconsidered the data of Evans and Black (1956), and found that initiation dates during 4 years were clearly correlated with temperatures during 2 April–6 May for mallards and 16 April–27 May for gadwalls. The analogous relation for blue-winged teal was not evident. We also examined Bengtson's (1972) data for duck populations in Iceland. The dates of first initiation for mallards and gadwalls during 9 years of study were related to mean temperatures in May ($r = -0.80$ for mallards, $r = -0.72$ for gadwalls).

Several factors have been implicated in controlling the onset on breeding in waterfowl and other birds. Väisänen (1974) suggested that laying dates are partly fixed by heredity and are modified by environmental conditions and the age of the bird. The individual consistency of laying date, perhaps under genetic control, was supported by Perrins (1970), Spurr and Milne (1976), and Batt and Prince (1979). Environmental conditions include photoperiod (Marshall 1961; Raveling 1978), access to nesting and feeding sites (Marshall 1961; Perrins 1970; Krapu and Doty 1979), and weather, which may have direct effects on birds and indirect effects through changes in the nesting habitat and food resources (Marshall 1961; Väisänen 1974; Raveling 1978; Krapu and Doty 1979). The importance of age of nesting female on initiation of egg laying has been suggested by Coulter and Miller (1968), Krapu and Doty (1979), and others.

Peak Hatching Dates

A measure of the progress of the nesting season is the peak, or median, hatching date—the date by which 50% of all observed hatchings occur. We had adequate information on peak hatching dates for all four species at Salyer and for the gadwall and blue-winged teal at Woodworth.

We sought to determine relations between peak hatching dates and weather, as measured by mean temperatures during 23 April–3 June, the period of most active nesting. We also looked for correlations with arrival dates, and explored two hypotheses:

(1) That a late nesting season in one year will result in a delayed nesting season the following year. The reasoning behind this idea is that if ducks cannot breed until they attain a certain age, such as 9 months, then a late season one year can result the next year in a large proportion of yearlings not capable of breeding until later in the season. Thus, the nesting season will be delayed.

(2) That a year with high production of young will cause a delayed peak hatching the next year. This hypothesis is based on the observation that yearling ducks typically begin nesting later than adults (Coulter and Miller 1968). Thus, a year with high production of

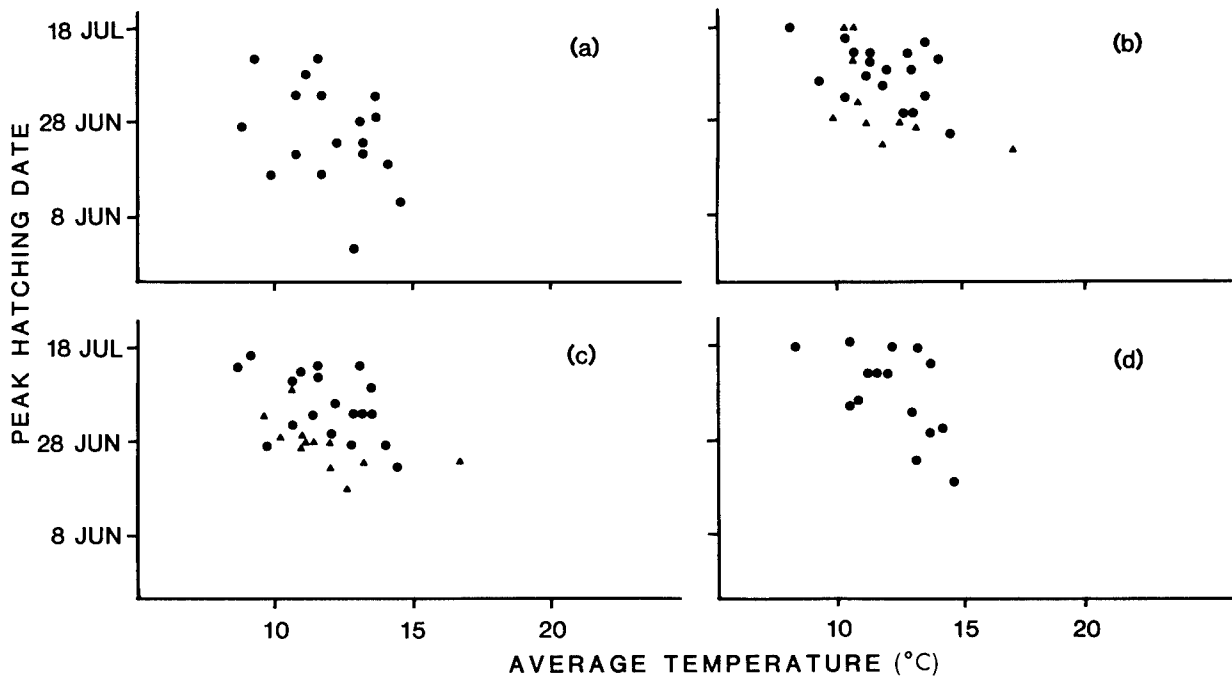


Fig. 3. Peak hatching date in relation to average temperature ($^{\circ}\text{C}$) during 23 April–3 June for mallard (a), gadwall (b), blue-winged teal (c), and redhead (d); dots denote Salyer, triangles denote Woodworth.

young will, if the young return to the nesting area, be followed by a year with a high proportion of yearlings in the breeding population, and thereby a delayed peak hatching date.

Peak hatching dates were also closely correlated with the date of initiation of first nest. It is difficult to separate the effects of one variable from the other because both variables measure the phenology of the nesting season. For this reason, we considered the two variables in combination.

Mallard

The median peak hatching date for mallards at Salyer was 25 June (Table 2). The peak hatching date was late when mean temperatures during 23 April–3 June were low (Fig. 3a) and when initiation was late; the effects were jointly significant at $P = 0.005$. The delay in peak hatching date averaged 0.99 day per Celsius degree difference in mean temperatures during that period, and 0.82 day for each day delay in initiating the first nest (Table 4).

Arrival date, the previous year's peak hatching date, and the previous year's production did not significantly affect peak hatching date.

Gadwall

Median peak hatching dates for gadwalls were 9 July

at Salyer and 29–30 June at Woodworth. Peak hatching dates of gadwalls were closely related to mean temperatures during 23 April–3 June (Fig. 3b). The coefficient of temperature was similar to the mallard, with 1.04 days delay per Celsius degree difference in mean temperatures, but the coefficient of initiation date was only 0.34 day (Table 4). Moreover, after the difference due to temperature was accounted for, peak hatching dates at Woodworth averaged 6.0 days earlier than at Salyer ($P < 0.05$).

Arrival date, the previous year's peak hatching date, and the previous year's production were not significantly related to peak hatching date.

Blue-winged Teal

Median peak hatching dates for blue-winged teal were 4–5 July at Salyer and 29 June at Woodworth. The blue-winged teal responded to mean temperatures during 23 April–3 June ($P = 0.05$; Fig. 3c), but date of first nest initiation was not influential ($P > 0.10$). The coefficient of temperature was -1.56 (Table 4).

After adjustment for mean temperatures, the peak hatching date was about 8.1 days earlier at Woodworth than at Salyer ($P < 0.01$). Effects of arrival date, and the previous year's production and peak hatching date were not significant with respect to peak hatching date.

Table 4. Coefficients of regression equations relating peak hatching date to mean temperature during 23 April-3 June, and to initiation date of first nest.

Species	Mean temperature ^a	Initiation date ^b
Mallard	-0.99	0.82
Gadwall	-1.04	0.34
Blue-winged teal	-1.56	0.13
Redhead	-2.45	0.52

^aDays per Celsius degree difference.

^bDays delay in peak hatching date per day delay in initiation date.

Redhead

The median peak hatching date for redheads at Salyer was 12 July. Redheads exhibited a strong association with weather (Fig. 3d) and date of first initiation ($P = 0.0001$). The peak hatching date was delayed 2.45 days for each Celsius degree decrease during 23 April-3 June, and 0.52 day for each day delay in initiating the first nest (Table 4).

There was no evidence for any effect on peak hatching date due to arrival date, or the previous year's productivity or peak hatching date.

General

All four species showed consistent relations between mean temperatures and peak hatching dates (Table 4). The four coefficients were roughly similar, varying from -0.99 to -2.45 days per Celsius degree change during 23 April-3 June.

Delays were also associated with late initiations of first nests; coefficients suggested that, for every day initiation of the first nest was delayed in a nesting season, the peak would be set back by 0.13-0.82 day. The association between mean temperatures and date of first nest initiation made it impossible to determine the individual effects of those variables on peak hatching date.

The two species for which we have data from both Salyer and Woodworth showed that the more southern location had slightly but significantly earlier peak hatching dates, after temperature differences were accounted for. We have no evidence that arrival dates, the previous year's productivity, or the previous year's peak hatching date influenced peak hatching dates.

Other authors (Yocom and Hansen 1960; Newton and Campbell 1975) have observed delayed nesting peaks in years with cooler springs. An analysis of Yocom's (1950) data yielded consistently negative correlations between peak hatching dates of four species and mean temperatures during April and, especially, May. Evans and Black (1956) recorded somewhat later nesting peaks by gadwall and blue-winged teal in 1950,

a year with below-normal temperatures during late April and May, but the mallard was not noticeably affected. Sorensen's (1978) data produced no relation between median hatch date and temperature. Sowls (1955) found that mallard and blue-winged teal nesting peaks were about 11 and 17 days later, respectively, in 1950 than in 1949. Temperatures during 15 April-30 May were 4 degrees Celsius lower in 1950 than in 1949. That difference was in the anticipated direction but was greater than would be predicted from the regression equation developed here.

Langford and Driver (1979) attempted to quantify relations between mallard nest initiations and temperatures. They estimated that a 1 Celsius degree change in minimum temperature during April resulted in a change in the mode of nesting dates of 2.0-2.4 days.

Delayed peaks of nesting can be caused by any of the earlier-described factors that influence the date of first nest. In addition, delayed peaks can result from interrupted nesting effort, sometimes ascribed to periods of low temperatures (Dane 1966; Dane and Pearson 1971; Dzubin and Gollop 1972).

Span of Nesting

An important attribute of duck nesting is the rapidity with which it is completed. The distribution of initiation dates over time indicates how uniformly the birds in the population initiate nests and re-nest. A species that makes only one nesting attempt, and is in relative synchrony, will exhibit a very short span of nesting. A species that has staggered nest initiation dates and considerable re-nesting will have a longer span of nesting.

We define the central span of nesting to be the interval from the date on which 10% of observed nestings began to the date on which 90% of them began. The span thus includes the central 80% of observed nestings.

We explored three hypotheses in our analysis of these data:

(1) That warm weather early in the nesting season will prompt nesting and thereby result in relative synchrony and a short span of nesting. Conversely, cooler weather will inhibit some individuals in the population, who will await more optimal nesting conditions. Other individuals will initiate nests anyway, and the resulting heterogeneity will be reflected in a longer span of nesting.

(2) That precipitation later in the nesting season will induce re-nesting among unsuccessful hens, thereby prolonging the nesting season. Conversely, dry weather at that time will tend to curtail further nesting.

(3) That a late nesting season, regardless of the cause, will shorten the span of nesting, because hens

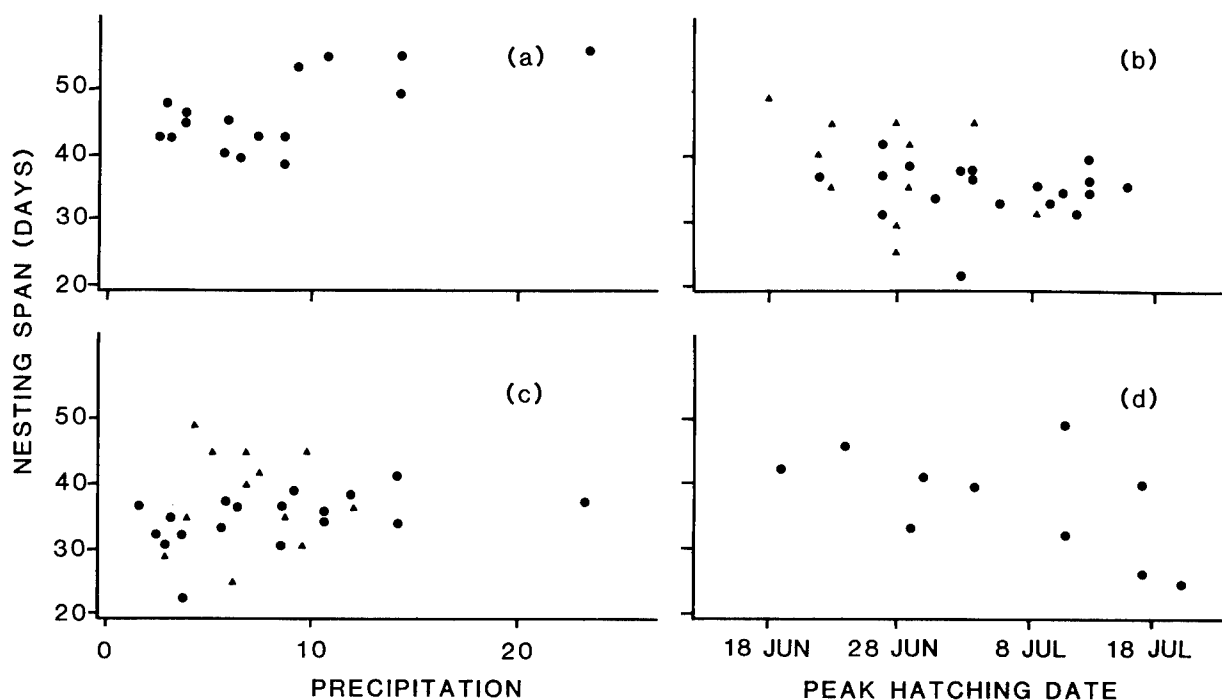


Fig. 4. Nesting span in relation to total precipitation (cm) during 23 April-3 June, and peak hatching date; mallard (a), blue-winged teal (b and c), redhead (d); dots denote Salyer, triangles denote Woodworth.

tend not to initiate nests after a certain date. This hypothesis was investigated by comparing the span with the peak hatching date.

Mallard

The average span of nesting for mallards was 46.6 days at Salyer (Table 2). The span was related to total precipitation during 23 April-3 June (Fig. 4a) and increased an average of 0.72 day for every centimeter of precipitation received during that period ($P = 0.003$).

No appreciable association occurred between mallard span of nesting and either mean temperatures during earlier weeks or the peak hatching date.

Gadwall

The average span of nesting for gadwalls was 32.9 days at Salyer and 30.6 days at Woodworth. The span did not appear related to mean temperature or precipitation during the usual nesting season, or to peak hatching date.

Blue-winged Teal

Eighty percent of blue-winged teal nests were initiated during a period averaging 34.7 days at Salyer and 38.1 days at Woodworth.

The relation between nesting span and peak hatching date was significant ($P = 0.03$, Fig. 4b). The average span decreased 0.31 day for each day delay in the peak. The relation between teal nesting span and precipitation during 23 April-3 June was suggestive (Fig. 4c), with a coefficient of 0.36 day per centimeter of precipitation ($P = 0.12$).

Redhead

Nesting span for redheads averaged 37.7 days at Salyer, but was 0.41 day shorter for each day delay in the peak nesting date ($P = 0.10$; Fig. 4d).

General

Average span of nesting varied among species, and was shortest in the late-nesting gadwall, intermediate in the blue-winged teal and redhead, and longest in the mallard, the earliest species to initiate nesting.

We detected no effects on the nesting span from mean temperature during the nesting season. Some authors (Dane 1966; Dzubin and Gollop 1972) noted that brief periods of cold weather interrupted nesting activities and occasionally caused bimodal nesting curves, which can lead to elongated nesting spans. Sorensen's (1978) data for mallards, however, do not suggest shorter nesting spans in warmer seasons but,

like ours, are based on average temperatures for long periods of time, which may not be sensitive to short periods of cold weather than can interrupt nesting and extend the span.

The suggestion that precipitation will encourage continued nesting and renesting was buttressed by evidence from the mallard and blue-winged teal. Both species had longer nesting spans during years of above-average precipitation during 23 April-3 June, the mallard by 0.72 day per centimeter of rain, and the blue-winged teal by 0.36 day.

For the blue-winged teal and redhead, nesting seasons that were later than usual resulted in shorter nesting spans. For each day the peak hatch date was delayed, the nesting span was shortened by 0.31 day in blue-winged teal and 0.41 day in the redhead. Keith (1961) and Raveling (1978) also observed that nesting seasons were more compressed in late seasons than in normal ones.

The duration of the nesting season thus seems to be affected by several variables whose interactions made interpretation difficult. Cold periods have been shown to interrupt breeding and prolong the nesting period. Precipitation that occurs during the breeding season presumably maintains wetlands in good condition and prolongs nesting. The analysis presented here for blue-winged teal and redheads supports other observations of shorter breeding seasons in years with late nest initiations.

Productivity

The brood to pair ratio, despite various drawbacks, is the most widely known and used index to productivity, and is perhaps the best currently available. The following analysis is based on brood to pair ratios for 14 years at Salyer and 13 years at Woodworth (Table 3). For comparability, ratios were multiplied by 1,000 at Salyer and by 100 at Woodworth.

To determine what effect weather had on the productivity rates, we examined the data relative to mean temperatures and precipitation totals during various intervals in the breeding season.

Mallard

Mallard productivity indices averaged 10.3 at Salyer and 27.1 at Woodworth. The different methods of counting broods rendered between-area comparisons impossible. Yearly variation was considerable; coefficients of variations (CV) were 72% at both areas.

Rates of mallard productivity at Salyer varied with mean temperature during 23 April-3 June (Fig. 5a). The expected increase in the brood index was 2.4 for every Celsius degree increase in temperature ($P < 0.02$). The effect of precipitation was nonsignificant. No relation between mallard productivity rates and weather variables was detected at Woodworth.

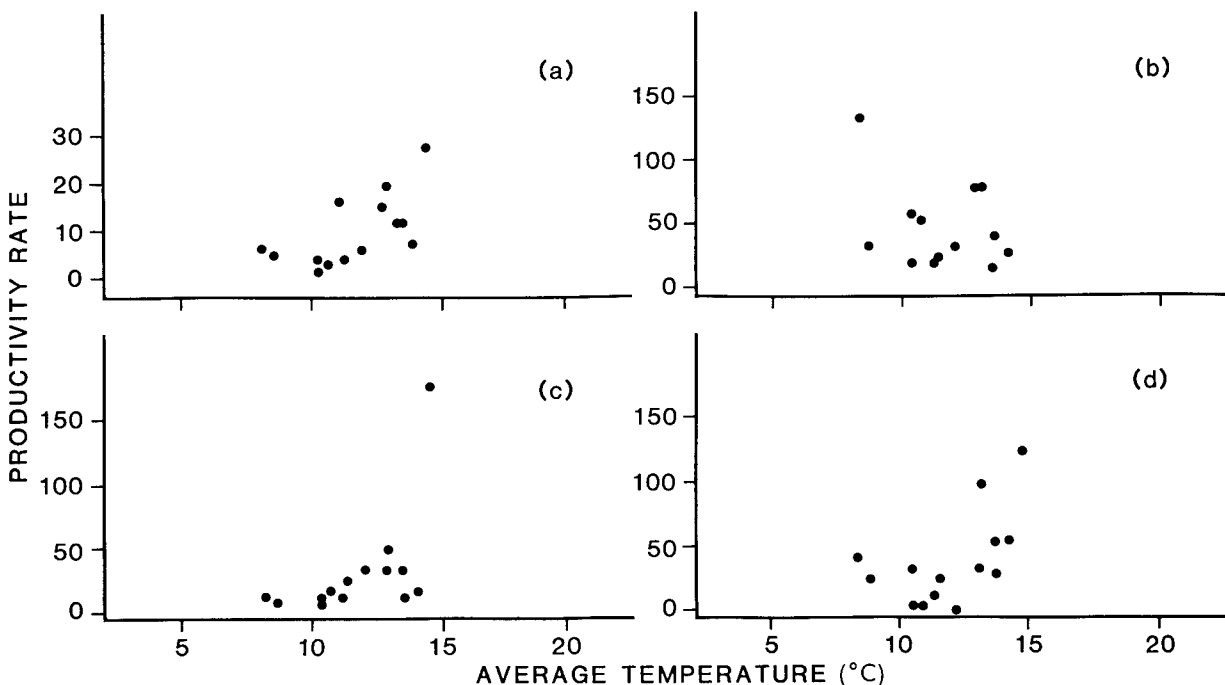


Fig. 5. Productivity (brood to pair ratio \times 1,000) at Salyer in relation to average temperature ($^{\circ}$ C) during 23 April-3 June; mallard (a), gadwall (b), blue-winged teal (c), and redhead (d).

Gadwall

Gadwall productivity indices averaged 65.3 (CV = 110%) at Salyer and 36.0 (CV = 59%) at Woodworth. We found no correlation between gadwall productivity rates and weather variables at either study area (Fig. 5b).

Blue-winged Teal

Productivity rates for the blue-winged teal averaged 31.9 (CV = 135%) at Salyer and 39.4 (CV = 53%) at Woodworth. At Salyer, these rates were significantly ($P < 0.05$) related to mean temperatures during 23 April–3 June (Fig. 5c), but much of the correlation was due to an extreme value in 1952, a warm year with an unusually large brood to pair index. With that year omitted from our data the regression was marginally significant ($P = 0.06$) and the rate of change was 3.7 per Celsius degree. Precipitation had no noticeable effect on the brood to pair counts.

No association between blue-winged teal productivity and weather variables was noted in the Woodworth data.

Redhead

At Salyer, redhead productivity indices averaged 38.5 (CV = 93%). Woodworth data were not examined because the pair populations were too small to base a productivity rate on.

The Salyer data displayed a relation to mean temperatures during 23 April–3 June (Fig. 5d). The productivity index of this species varied 10.0 for each Celsius degree change in mean temperature ($P = 0.04$). No effect of precipitation was discernible.

General

The productivity rate, unlike the other characteristics we investigated, yielded far different results from the two study areas. We attribute the absence of noticeable weather effects at Woodworth to a masking by high but variable rates of predation. It is widely believed that predation had intensified from the period when Salyer data were gathered to that when Woodworth data were gathered.

At Salyer, all species except the gadwall exhibited a significant correlation between brood to pair ratios and mean temperatures during 23 April–3 June. The regression coefficients, expressed as a percentage of the average index, were 0.68% for mallard, 0.32% for blue-winged teal (1952 excluded), and 0.72% for redhead. These values were highest for the mallard and redhead, which began nesting first, lower for the teal, which initiated next, and nonsignificant for the gadwall, the latest to nest.

This analysis suggests that productivity at Salyer was higher during years with warm mid-season weather, with the exception of the late-nesting gadwall.

Other researchers have associated reduced productivity with climatic features, notably delayed, cool springs. Nilsson (1974) found mallards more productive in years with warm April weather. Makepeace and Patterson (1980) reported higher survival of shelduck (*Tadorna tadorna*) ducklings in years with more warm days in the season, and in years with fewer windy days. The number of rainy days was not significantly associated with duckling survival. Lensink (1973) found, as we did, that delayed, cool springs affected the productivity of early-nesting ducks more than later-nesting species. Milne (1976) suggested that, among Arctic-nesting waterfowl, dabbling ducks were more sensitive to low spring temperatures than were diving ducks.

Two published reports contained sufficient detail for us to examine their data in a comparable manner. Evans and Black (1956) provided productivity data and temperatures for 1950–53. Three years had similar temperatures during 23 April–3 June, but 1950 was somewhat cooler. Productivity rates of mallards were noticeably lower that year, but those of blue-winged teal and gadwall were not appreciably different from the other years. These results are generally consistent with ours. A reanalysis of Smith's (1971) data showed that brood to pair ratios during 1953–58 were positively correlated with minimum temperatures during April and May for mallard, blue-winged teal, and all species combined. Regression coefficients were largest for the mallard, suggesting greater sensitivity of that early-nesting species.

Low temperatures during the breeding season can reduce productivity by affecting breeding adults or young. Effects on the breeding pair include nonnesting by some of the population (Lensink 1973; Milne 1976), late nesting (discussed earlier), and reduced clutch size, which can depress brood to pair ratios if smaller broods are less likely to survive or to be seen than larger ones.

Direct effects of low temperatures include death from exposure, increased vulnerability to predators, and reduced opportunity to feed adequately. Boyd and Campbell (1967) observed greater duckling losses during periods of cold, wet weather, and Hildén (1964) and Bengston (1972) found that newly hatched ducklings were particularly susceptible. Seymour (1982) observed a 1- or 2-day-old mallard duckling become separated from its mother and broodmates, and die within 60 min of exposure to 4°C air and 3°C water temperatures.

Increased susceptibility to predation during periods of cold has not been reported; however, reduced opportunity to feed was noted by Hildén (1964), who stated that surface feeding becomes more difficult in cold, windy weather. This phenomenon could partly account for the greater susceptibility of dabbling ducks compared with that of divers.

Table 5. Correlation coefficients between brood size and breeding pair population, mean temperature during 21 May–1 July, and year.

Class and species	Pair population	Mean temperature (°C)	Year
I			
Mallard	-0.29	0.07	-0.49
Gadwall	-0.64 ^b	-0.15	-0.83 ^c
Blue-winged teal	-0.46 ^a	-0.47 ^a	-0.72 ^c
Redhead	-0.36	-0.04	-0.14
II			
Mallard	-0.62 ^b	-0.40	-0.56 ^b
Gadwall	-0.74 ^c	-0.45 ^a	-0.50 ^b
Blue-winged teal	-0.34	-0.63 ^c	-0.81 ^c
Redhead	-0.53	+0.77 ^b	+0.40

^a $P < 0.10$.

^b $P < 0.05$.

^c $P < 0.01$.

Koskimies and Lahti (1964) found differences among species with respect to cold-hardiness of newly hatched ducks, and postulated that cold-hardiness is an uneconomical strategy except in a relatively narrow zone of environmental conditions. They claimed that a low metabolic rate, associated with reduced adaptation to cold, is advantageous during normal weather in most breeding areas. Thus, the less cold-hardy species tend to be more adaptable and to have larger breeding ranges.

Brood Size

We used two measurements of brood size: average numbers of ducklings in broods of age Class I and of age Class II. Class I ducklings ranged in age from 1 day to about 18 days in mallards and gadwalls, 13 days in blue-winged teal, and 24 days in redheads (Gollop and Marshall 1954). Age ranges in days of Class II ducklings were 19 to 45 for mallards, 19 to 44 for gadwalls, 14 to 36 for blue-winged teal, and 25 to 54 for redheads. These data, from Salyer, span 7 to 16 years depending on species and age class. Brood size averages are based on a minimum of five broods; most averages involved much larger sample sizes. The Class I brood size reflects the number of eggs in a clutch, the proportion of those that hatch, the proportion of hatched ducklings that reach water, and the survival of those ducklings until time of census. The Class II brood sizes reflect these factors, as well as survival from Class I and Class II.

Although it is easy to conceive of numerous hypotheses relating brood size to various aspects of weather, we were unable to detect any relation between precipitation and brood size. Correlations between mean

temperatures and brood size were at least suggestive. Additionally, brood size was correlated with breeding population and with year, the correlation with year suggesting a trend in average brood size.

We considered mean temperatures during 21 May–1 July, when eggs in most nests were hatched and young brought to water. Correlation coefficients between brood size and pair population size, mean temperature, and year are given in Table 5. Intercorrelations exist between certain of the explanatory variables (e.g., population size and year) because most species generally increased in number during the course of the study. These intercorrelations confounded our analysis of effects on brood size.

Mallard

Average brood sizes for mallards were 6.8 in Class I and 6.5 in Class II (Table 6). Class I brood size was not significantly correlated with population size, mean temperature, or year (Table 5). Class II brood size was correlated with population size (Fig. 6a) and year (Fig. 7a). The effect of population size was more marked, and the effect of year, after accounting for the effect of population size, was no longer significant ($P = 0.31$).

Gadwall

Gadwall brood sizes averaged larger than those of mallard—7.3 in Class I and 7.2 in Class II. Class I brood size was correlated with population size (Fig. 6b) and, especially, with year (Fig. 7b). The effect of population size was not significant after accounting for the trend, which suggested a decline in brood size of 0.11 duckling per year. Class II brood size was correlated, in decreasing order, with population size

Table 6. Summary statistics of average Class I and Class II brood sizes at Salyer.

Class and species	n ^a	Mean	SD ^b
I			
Mallard	11	6.8	0.8
Gadwall	17	7.3	0.7
Blue-winged teal	17	7.0	1.0
Redhead	14	6.5	1.1
II			
Mallard	15	6.5	1.3
Gadwall	16	7.2	0.6
Blue-winged teal	16	6.6	1.4
Redhead	7	6.5	0.7

^an = number of years.

^bSD = standard deviation.

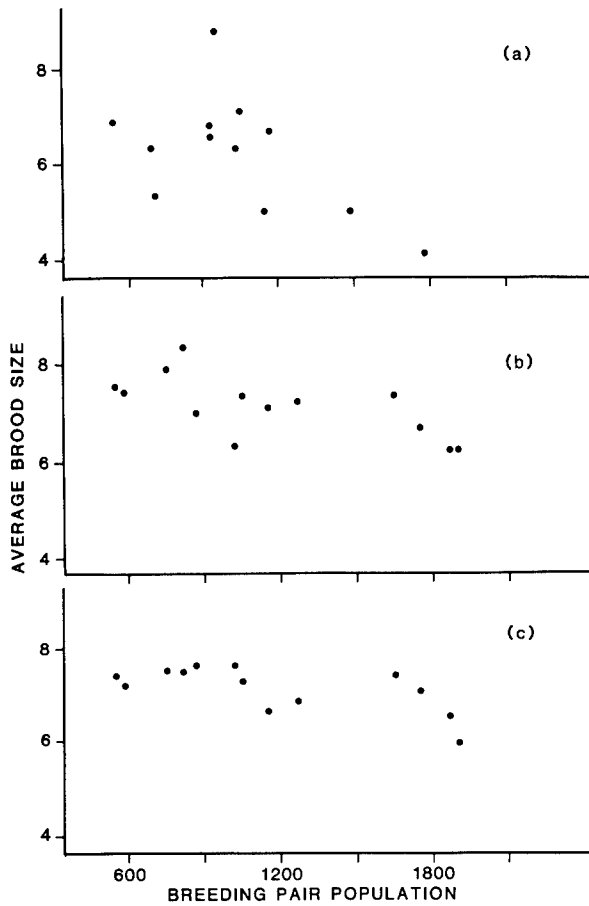


Fig. 6. Average brood size in relation to breeding pair population; mallard, Class II (a); gadwall, Class I (b); gadwall, Class II (c).

(Fig. 6c), year (Fig. 7c), and mean temperature. The effect of population size dominated, and marginal effects of other variables were not significant.

Blue-winged Teal

Brood sizes of blue-winged teal were intermediate between those of mallard and gadwall—7.0 in Class I and 6.6 in Class II. Class I brood size trended downward (Fig. 7d), and correlated to lesser extents with mean temperature and population size. Class II brood size was significantly associated with year (Fig. 7e) and mean temperature (Fig. 7f). The decline with year averaged 0.23 Class II duckling annually.

Redhead

Data on redhead brood size were limited; both classes averaged 6.5 ducklings. None of the correlations with Class I brood size was significant, and the number

of Class II broods was inadequate to examine any hypotheses.

General

Brood size tended to be largest and least variable among gadwalls. Blue-winged teal had the next largest broods; mallards and redheads had the smallest.

Intercorrelations among explanatory variables, notably year and breeding pair populations, obscured our analysis. Class I brood sizes declined for most species during the period of study. The decline can be attributed only partly to increased breeding pair populations. Weather was not strongly associated with Class I brood size; only blue-winged teal demonstrated even a marginal relation with mean temperature.

Class II brood sizes were negatively correlated with breeding pair populations among all species; correlations attained significance among mallards and gadwalls. Average brood sizes of all dabbling species declined during the course of the study, but only in blue-winged teal was this effect not accounted for by concurrent population increases. All dabblers tended to have smaller Class II broods during years when temperatures during 21 May–1 July were above normal; the significance of this effect varied among species.

Many investigators have identified cold and wet weather as stressful to ducklings, especially young ones (Hildén 1964; Koskimies and Lahti 1964; Boyd and Campbell 1967; Bengtson 1972; Seymour 1982). Our data did not confirm this association, but the weather data we used—average temperature over extended periods—may have been too crude to detect short-term inclement spells that could be fatal to young ducklings. Instead, we detected some associations between above-normal temperatures during late May and June and reductions in brood size, particularly in Class II. An analysis of Stoult's (1971) mallard and blue-winged teal data also showed negative correlations between average temperatures in June and Class I and Class II brood size:

	Mallard (10 years)	Blue-winged teal (9 years)
Class I	$r = -0.478$ ($P = 0.17$)	$r = -0.312$ ($P = 0.43$)
Class II	$r = -0.691$ ($P = 0.02$)	$r = -0.477$ ($P = 0.20$)

Several investigators (Dane 1966; Perrins 1970; Batt and Prince 1979; Krapu 1981) have shown that clutches laid later in the season are smaller than those laid earlier, and that clutches laid during years with cool springs average smaller than those of normal years (Krapu and Doty 1979). We anticipated that this effect might carry through to brood size, but in our analysis we found no association between brood size

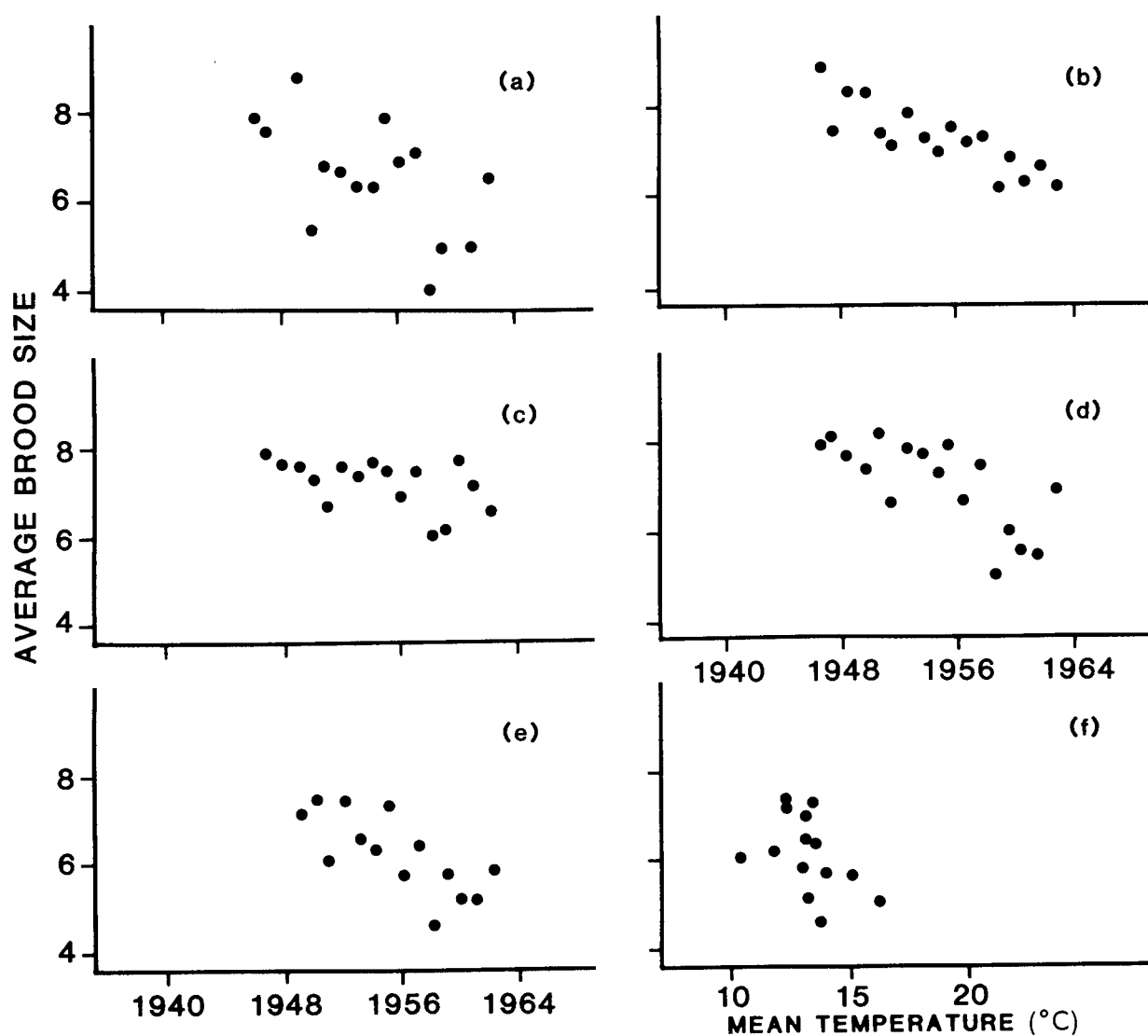


Fig. 7. Average brood size by year (a-e), and average brood size in relation to average temperature ($^{\circ}\text{C}$; f) during 21 May-1 July; mallard, Class II (a); gadwall, Class I (b); gadwall, Class II (c); blue-winged teal, Class I (d); and blue-winged teal, Class II (e and f).

and date of peak hatch, a measure of the phenology of the season.

In addition, we detected a significant decline in average brood sizes during 1947-62. Some of the decline can be attributed to increased breeding pair populations of the dabblers. The dependency on population size could reflect interference either among breeding pairs or among ducklings. Dzubin (1969) suggested that large pair populations might result in many nests located at considerable distances from brood water, and thereby lower brood survival. Makepeace and Patterson (1980) reported that the daily mortality of shelduck (*Tadorna tadorna*) ducklings increased with the density of broods, as did aggressive interactions. The additional variability due to year is difficult to explain,

but could result either from changes in methods used to count ducklings or, more likely, from alterations in the habitat used by breeding adults and ducklings or in the predator composition. In addition, increased predation might have resulted in greater contributions of renests, which contain fewer eggs than do initial clutches. Brood sizes of the redhead were not related to pair populations and did not decline during the study period.

Conclusions

Data presented here indicate that weather plays a critical role in the arrival and breeding of waterfowl in

the northern plains. Many of our conclusions were supported by reports of other investigators or by reanalysis of their data. Further, we tried to quantify relations between various aspects of weather and important components of waterfowl breeding. Such quantification can be particularly useful in developing models of waterfowl productivity. The observational nature of the data used in this report contrasts with data from experimental studies; the long period over which these data were obtained should complement experimental findings, which are typically of short duration, as well as suggest hypotheses for productive experimental study.

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Keywords: Mallard, Gadwall, Blue-winged teal, Redhead, productivity, breeding biology, weather, North Dakota, waterfowl, duck.

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A list of current *Technical Papers* follows.

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